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RESPONSE DIVERSITY FOR CLIMATE-RESILIENT FORAGE CROPS

Hanna Mäkinen

ACADEMIC DISSERTATION

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Main supervisor:
Professor Helena Kahiluoto
Professor of Sustainability Science
Lappeenranta University of Technology (LUT)
Adjunct Professor of Agroecology
University of Helsinki
LUT School of Energy Systems, LUT Lahti
FI-15140 Lahti, Finland

Supervisors:
Adjunct professor Perttu Virkajärvi
Natural Resources Institute Finland
FI-71750 Maaninka, Finland

Professor Juha Helenius (responsible Professor)
Professor of Agroecology, University of Helsinki
Department of Agricultural Sciences/Agroecology
FI-00014 University of Helsinki, Finland

Reviewers:
Dr. Mats Høglind
Norwegian Institute of Bioeconomy Research (NIBIO), Norway

Professor Miroslav Trnka
Czechglobe, Global Change Research Institute CAS
Department of Climate Change Impacts on Agroecosystems, ÚVGZ AV ČR, v. v. i., Czech Republic

Opponent: Dr. Kaija Hakala

Custos: Professor Juha Helenius

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CONTRIBUTION

I The author was the corresponding author. She was the main planner of the research and made a significant contribution to all parts of the study. She was in charge of identifying the required long-term data, conduction of the literature search, and interpretation and presentation of the results as well as writing of the manuscript. She coordinated the team-based statistical analyses, which were jointly planned and interpreted.

II The author was the corresponding author. She made a significant contribution to all parts of the study, including planning of the research. She was in charge of the literature search, coordination of the team-based statistical analyses, interpretation and presentation of the results, and the writing of the first draft of the manuscript as well as the finalizing of it.

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ABSTRAKTI

Ilmastonmuutoksen myötä vaihtelu ja epävarmuus ilmastossa ja säässä yleistyvät. Perinteisen sopeutumistutkimuksen rinnalle tarvitaan sopeutumiskykyisyyttä ja satovarmuutta korostavia näkökulmia. Monimuotoisuus liitetään sopeutumiskykyyn ja resilienssiin. Vaikuttavinta monimuotoisuutta ympäristönmuutoksessa näyttäisi olevan vasteiden monimuotoisuus, joka on toiminnallisen ryhmän sisäistä monimuotoisuutta vasteissa muutokselle ja vaihtelulle. Nurmet ovat Suomen yleisin pellonkäyttömuoto, ja nurmirehut ovat maidontuotannon ja märehtijäpohjaisen lihantuotannon kulmakivi. Tutkimuksen tavoitteena on kvantifioida säävastemonimuotoisuutta empiirisesti nurmirehukasveilla ja niiden eri lajikkeilla keinona arvioida satovarmuutta ilmastonmuutoksessa. Lisäksi kehitettiin vastemonimuotoisuus-indeksi, RD-indeksi, jonka käytännönmerkitystä havainnollistettiin. Nurmikasvien sadonmuodostukselle hypoteettisesti kriittiset, nurmen fenologiseen kehitykseen kytkeytyvät säätekijät valittiin kirjallisuuteen ja kokemukseen perustuen ja niiden vaikutus testattiin empiirisesti nurmen karaistumiskaudella, talvehtimiskaudella ja kasvukaudella. Tutkimuksessa käytettiin aineistona Luonnonvarakeskuksen (entisen MTTn) virallisia lajikekokeita: timotein (*Phleum pratense* L.), nurminadan (*Festuca pratensis* L.), ruokonadan (*Festuca arundinacea* L.), rainadan (*Festulolium* L.), puna-apilan (*Trifolium pratense* L.) sekä Italian raiheinän (*Lolium multiflorum* L.) ja niiden eri lajikkeiden (126 lajiketta) tuloksia. Lisäksi käytettiin Ilmatieteenlaitoksen sääaineistoa (vuosilta 1979–2012). Lineaarisen sekamallin avulla määritettiin koepaikan, vuoden ja säätekijöiden vaikutus sadon määrään. Analyysin toisessa vaiheessa lineaariseen sekamalliin lisättiin koepaikan, vuoden ja säätekijöiden ohelle maalajit. Ensin tutkittiin lajien sisäistä satovasteiden monimuotoisuutta yksittäisille säätekijöille hyödyntäen vain uusimpia nurmikasvilajikkeita. Ilmeni että uusimpien lajikkeiden erilaisuus vasteissa säähän oli vähäistä: erityisen samanlaisiksi säävasteiltaan osoittautuivat timotein ja nurminadan lajikkeet. Sen sijaan rainadan lajikkeet osoittautuivat eroavan toisistaan säävasteissa, joka indikoi sen sopeutumiskykyisyyttä ilmastonmuutoksessa.

Pääkomponenttianalyysillä säätekijät ryhmiteltiin, ja nurmilajit ja lajikkeet klusteroitiin säävasteisiin perustuneista pääkomponenttipisteistä. Nurmikasvilajeilla ja lajikkeilla osoitettiin esiintyvän käytännöllisesti merkittävää säävastemonimuotoisuutta. RD-indeksin arvo säävastemonimuotoisuudelle, mitattuna tunnistettavissa olevien funktionaalisia lajiryhmien ja lajikkeiden samanlaisina vasteina, oli 10 poikki maalajien. RD-indeksin kasvu vähensi säävastesatovaihtelua.

Säävastemonimuotoisuus-indeksi vaihteli eri ilmasto x maalajien välillä: karkeilla kivennäismailla 4, savella 9 ja orgaanisilla mailla 8. Nurmikasvien ja –lajikkeiden säävastemonimuotoisuuden riippuvuus maalajista osoittaa huomionarvoiseksi sen, että suunniteltaessa ilmastonmuutokseen sopeutumista on kiinnitettävä huomioita muutoksiin maaperän ja ilmaston yhdysvaikutuksessa.

ABSTRACT

Climate change is characterized by uncertainty in climate and increasing variability in weather. In addition to traditional 'predict and adapt' approaches of preparing for projected average long-term change in climate, approaches addressing adaptive capacity and system resilience are required. Diversity is associated with enhanced stability and resilience in the face of climate change. However, any kind of diversity does not necessarily enhance resilience, but the diversity of responses is critical to resilience. Such response diversity means that the ability to react to changes and variability differs within a functional group. In this thesis, response diversity was empirically assessed using forage crops, a response diversity index (RD-index) was constructed and the practical significance of the RD-index was demonstrated. Forage crops were chosen for the studies because they are a cornerstone of Finnish dairy and beef farming. The following species and their cultivars were included: timothy (*Phleum pratense* L.), meadow fescue (*Festuca pratensis* Huds.), tall fescue (*Festuca arundinacea* Schreb. syn. *Lolium arundinaceum* Schreb.), festulolium (*Festulolium pabulare*), Italian ryegrass (*Lolium multiflorum* L.) and red clover (*Trifolium pratense* L.). The analyses started with testing the effect of the hypothetically critical agro-climatic variables on forage crop yield performance using plant data from the Official Variety Trials of Natural Resources Institute Finland (126 cultivars) and the weather data of the Finnish Meteorological Institute from 1979 to 2012 that was matched to the phenology of the crops. A linear mixed model was used to determine the effect of the site, year and weather on crop yields (I, II). In the second round of analyses, the three-way interaction of cultivars, soil types and weather were analysed using mixed models (III). Within-species diversity of responses to individual weather variables was firstly investigated for the modern set of forage crop cultivars. The results revealed that in these, within-species diversity in response to weather was generally low, particularly within the modern set of timothy and meadow fescue cultivars. On the other hand, the set of modern festulolium cultivars showed higher levels of differences in responses, which indicates their greater capacity to cope with climate change (II).

Principal component analysis was used to determine common weather patterns, and forage crops and their cultivars were clustered based on the scores of the principal component analysis (I, III). Response diversity to the critical weather patterns within the set of forage crop species and cultivars was found. The value of the RD-index, measured as numbers of identifiable functional groups of species and cultivars with similar yield responses, was 10 across the soil types. An increase in RD-index decreased the yield response variation. The practical significance of complementarity of yield

responses of forage crops and their cultivars represents an option for the enhancement of climate resilience of feed production. The RD-index of forage crops and their cultivars varied from one climate–soil type pattern to another, with the following RD-index values: coarse mineral soils = 4, clay = 9, organic soils = 8 (III). Due to the demonstrated dependency of crop responses to climate change on soil type, attention should be given to the plausible shifts in soil–climate combinations when planning adaptation.

1 INTRODUCTION

1.1 A NEED FOR CONSIDERING RESILIENCE IN CLIMATE CHANGE ADAPTATION

Climate change has brought considerable uncertainty to human activities. The sensitivity of agriculture to change in climate is widely recognized. Climate variability has occurred throughout history (Ray et al. 2015) and continues to be the main source of fluctuation in food production (Christidis et al. 2014). The consequences of climate change are likely to be experienced more frequently, and they are becoming more costly (Stern et al. 2006). However, climate driven changes are hard to predict (Rötter et al. 2013) and uncertainty in climate change is significant. Therefore, traditional 'predict and adapt' approaches of preparing for projected average long-term change in climate may not be sufficient (Dessai et al. 2007). Food and feed are not easily (and not entirely) substitutable through the market if losses occur. Yield reduction and variation in annual yields have severe consequences at the farm level, and have harmful effects on the whole agricultural sector and food security. System resilience is likely to be crucial in ensuring the performance of ecosystem processes essential for humanity facing deep uncertainties (Holling 1973, Dessai et al. 2007, Folke et al. 2010).

1.2 THE CONCEPTS OF RESILIENCE AND STABILITY OF ECOSYSTEMS

What matters to the stability of ecosystems has fascinated ecologists for a long time. Stability in ecological literature refers to a wide range of phenomena, but it often refers to a system's dynamic stability or a system's resilience and ability to resist change (McCann 2000). Equilibrium stability considers that a system is stable when it returns to equilibrium after a disturbance. Holling (1973), held as the pioneer of resilience research, distinguished two dimensions of resilience: engineering resilience and ecological resilience. Engineering resilience was defined as the ability of a system to return to a state of equilibrium after a disturbance. This dimension of resilience concentrates on the speed of returning to equilibrium and the system's resistance to disturbances, and thus the focus is on stability close to an equilibrium state. The ecological dimension of resilience noticed that systems can move to an alternative domain of attraction through a regime shift: fluctuations can push the system over a threshold to another stability domain, where a regime is a dynamic state of a system with its characteristic stochastic fluctuations (Scheffer et al. 2001). Thus, the ecological dimension

of resilience emphasized the magnitude of disturbance the system can absorb before the system structure or control behaviours change (Holling 1973). Engineering resilience overlaps with ecological resilience in some regards, but ecological resilience emphasizes 'persistence, change, and unpredictability', whereas engineering resilience focuses on 'efficiency, constancy, and predictability' (Holling 1996). Despite the variety of interpretations, the ecological concept of stability is often associated with reduced (temporal) variability. In field experiments, stability is often measured as decreased variability of population or community densities. Variability considers the variance in population (or community) densities over a period (which can be measured as the coefficient of variation) (Tilman 1996, Hooper et al. 2005).

Although the concept of resilience originates from ecology, it has evolved to consider socioecological systems and is used as an approach or as a boundary object to analyse systems across disciplines (Brand and Jax 2007). One highly cited definition of socioecological resilience is proposed by Walker et al. (2004): 'Resilience is the capacity of a system to absorb disturbance and reorganize while undergoing change so as to still retain essentially the same function, structure, identity, and feedbacks—in other words, stay in the same basin of attraction'.

1.3 DIVERSITY, STABILITY AND RESILIENCE OF ECOSYSTEMS

Early ecological studies hold that ecosystems should be more stable in the face of environmental fluctuations as the diversity increases (Odum 1953, MacArthur 1955). The diversity–stability hypothesis has been debated by ecologists for decades (McCann 2000), and there is still disagreement about, and inconsistences in, the mechanisms behind and the interrelationship between ecosystem functioning (such as productivity) and diversity (Yodzis 1981, May 1974, Naeem and Li 1997, McCann 2000, Cardinale et al. 2007). The current understanding is that diversity contributes to ecosystem functioning and stability, at least on average (Tilman 1996, McCann 2000, Wardle et al. 2000, Bai et al. 2004, Isbell et al. 2015). The diversity–stability relationship at the community level of primary production is generally explained by the averaging effect, negative covariance effect and insurance effect (Yachi and Loreau 1999, McCann 2000). Empirical evidence from grasslands supports the idea that species diversity within an ecosystem correlates with the stability of biomass productivity of the community, measured as resistance to change and as return to equilibrium after disturbance (Tilman and Downing 1994, Tilman et al. 1996). This positive relationship at the community level occurs because different species in the plant communities respond differently to variations in environmental

conditions, and thus the sum of population responses stabilizes the community through time. Stability of community and ecosystem processes does not necessarily mean stability at the level of populations, rather the opposite as variability or responses in the populations actually seem to be the mechanism contributing to the stability of the community processes, i.e. processes at ecosystem level (Tilman 1996). Distinction between the stability of community composition (identity and relative abundances of the species) and stability of community/ecosystem processes is important, because changing community composition can be the main mechanism enhancing the stability of its processes (such as biomass production), whereas change in the composition can also be considered as reduced stability (May 1974, Tilman 1996, Hooper et al. 2005).

1.4 WHAT TYPE OF DIVERSITY MATTERS TO RESILIENCE?

All forms of diversity do not contribute to ecosystem stability and resilience equally. Species diversity represents the most widely adopted measure of diversity (for a synthesis, see Balvanera et al. 2006, Cardinale et al. 2007). Species diversity is usually measured as a combination of species richness and species evenness (Peet 1974), where richness is simply the number of species and evenness describes the similarity of species in their abundance. There are different measurements that quantify different phenomena of rarity and commonness of species (diversity indices can also be used for quantifying other forms of diversity, but interest is usually in species) in a given community. For instance, a common index in the field of ecology is the Shannon index (Shannon and Weaver 1949, Tuomisto 2010). Species diversity, however, lacks the ability to capture the functionality of the species in its ecosystem, and thus does not lend itself to analysis of the performance of the community, such as its stability of function in the face of change (Mori et al. 2013, Spasojevic et al. 2016). Hence, it has been proposed that functional diversity matters more than species diversity per se (e.g. Naeem and Li 1997, Díaz and Cabido 2001).

Functional diversity refers to 'the value and the range of those species and organismal traits that influence ecosystem functioning' (Tilman 2001). Or, as Hooper et al. (2005) and Mori et al. (2013) describe, functional diversity refers to the variation or dispersion of functionally different roles (or groups) within a system contributing to the same function, presupposing a link between diversity and ecosystem processes. A functional group is a collection of, for example, components or species that share some common attributes. The most generic groupings of course are the main trophic groups, the primary producers, the grazers, the predators and the decomposers. To study functional diversity, an appropriate level of functional grouping is always far

more detailed, context specific and needs to be defined by the investigator for the purpose of the study. Extinction of any functional group is likely to result in loss of ecosystem function, and the measure of functional importance is thus the impact size of the loss. Functional redundancy means overlapping of the functions, and describing the number of components (e.g. species) contributing in a similar manner to ecosystem functioning (Laliberte et al. 2010). This redundancy potentially provides insurance against change. The insurance hypothesis holds that species-rich communities insure ecosystems against decline in function because even if one species fails, the function can be compensated for by other species with a similar functional contribution. This effect is explained by, among other explanations, different responses by the functionally overlapping species to environmental change (Yachi and Loreau 1999, Loreau et al. 2001).

Functional redundancy may not necessarily ensure the high 'response diversity' that seems the most critical for resilience (Elmqvist et al. 2003, Mori et al. 2013). Response diversity refers to the diversity of responses to change in environment within a functional group, i.e. within the components (e.g. species) that have a similar function in the ecosystem (or agroecosystem) (Walker et al. 1999, Elmqvist et al. 2003, Mori et al. 2013) (or species with similar effect traits (Mori et al. 2013)). Response diversity contributes to functional compensation if one or more of the components performing a particular ecosystem service are lost, and it facilitates maintenance and successful reorganization of the functions while change is underway (Walker et al. 1999, Elmqvist et al. 2003). A system that contains a high degree of response diversity at various hierarchical levels is likely to be resilient to different stresses and to provide seeds for renewal (Elmqvist et al. 2003, Mori et al. 2013).

Current understanding of response diversity is inadequate, in terms of theoretical and empirical evidence (Mori et al. 2013). There are published examples of the value of response diversity to system performance under change or shocks from studies in ecological or agroecological communities, for instance in coral reefs (Nyström 2006), bees (Winfree and Kremen 2009), plant communities in rangelands (Walker et al. 1999), and rice (Zhu et al. 2000) and barley cultivation (Kahiluoto et al. 2014). These studies have not used the concept of response diversity in describing the trait diversity that was reported as important (but see Kahiluoto et al. 2014), and have not measured the degree or variability of such diversity in these various systems. Similarly, the value of response diversity to resilience in socioecological systems (e.g. Leslie and McCabe 2013, Tendall et al. 2015) has been argued for, but without assessment of the possible value of response diversity.

1.5 GENETIC DIVERSITY AND RESPONSE DIVERSITY IN AGRICULTURAL SYSTEMS

The hierarchical ecosystem levels can be defined, for example, as atoms, cells, organs, individuals, populations, species, communities, ecosystems, landscapes, regions and the ecosphere (Jørgensen 2012). Diversity is represented in all hierarchical organization levels: the molecular level, the genetic level, the cell and organ levels, the species level, the community level and the network and ecosystem level. All diversity in living beings refers to biodiversity (Jørgensen 2012). Agricultural systems include natural and semi-natural plant and animal species and communities, but agricultural systems differ from natural or semi-natural ecosystems in the sense that humans (breeders, farmers) can actively manage the diversity in agricultural systems, not only at field level but also at higher levels of organization, within farms and within the cropped landscape, region and the country.

Genetic diversity is the basis of the breeding of crops and cultivars. Utilization of different genetic pools ensures a sufficiently broad genetic basis for trait variation in breeding (Wilkins and Humphreys 2003). The gene and the environment and their interaction determine the phenotype of a crop. Crop traits are morphological or physiological characteristics that have an influence on crop performance. Phenotypic plasticity clearly affects the adaptability of species but it may lead to overestimation of the genetic variation (Charmet et al. 1997). The challenge for plant breeders is to select the adaptive genetic variation rather than the favourable phenotypic traits (Fjellheim et al. 2015). There exists a great interest in understanding the gene, genes and genetic mechanisms that are responsible for the traits of interest for breeding (Fjellheim et al. 2015, Sun et al. 2015). In order to improve the accuracy of estimated breeding outcomes, more recently DNA-based markers have started to be used alongside phenotype and the pedigree-based selections (Hayes et al. 2013).

Forage crops and their cultivars are the cornerstone of ruminants-based agricultural production, which has high economic significance in European agriculture, and in Finland, perennial grasslands are the most common land use of the utilized agricultural area (Natural Resources Institute Finland 2015). The greatest difference in the breeding of many cereals is that forage crop species tend to be more complicated species for breeding (timothy for instance due to its cross-pollinating nature and hexaploid set of chromosomes). In addition, lower financial investments are made for forage breeding because forages are resown only every 3 to 4 years (or even more rarely). The genetic links in desirable and undesirable genes and the effects of a minority of genes (direct, pleiotropic effects of genes) have an impact on one trait and therefore it is often important to assess all the traits in each generation in order to select better cultivars and prevent failures in breeding (Wilkins and Humphreys 2003).

Plant breeding programmes can be pursued either to narrow adaptation or extend adaptation under a considerable range of conditions (Finlay and Wilkinson 1963). Extensive adaptation means performance under different growing conditions that vary markedly between south and north Finland, particularly in terms of effective temperature sum accumulation, photoperiodic and winter conditions, as well as soil characteristics. Regarding timothy, the northern populations have the highest vernalization requirements and they have longer photoperiodic requirements than the southern populations (Fjellheim et al. 2015). Many cultivars have been bred for a specific northern location, whereas the origin of modern timothy cultivars is from a wider gene pool and they have been bred to perform well all over the country (Isolahti 2010).

Since the 1980s, grass breeding in temperate regions has focused on the quantity of forage dry matter (DM) yield, the quality of the yield and persistence (Wilkins and Humphreys 2003, Hayes et al. 2013). DM digestibility of yield is particularly important since it increases the energy content of forage feeds but also boosts the voluntary intake of forage feeds by ruminants. Digestibility is dependent on cell wall cellulose and lignin content and existence of oligosaccharide carbohydrates (Hayes et al. 2013). Forages and their cultivars tend to vary greatly in their digestibility in different cuts (Wilkins 1997). Breeding of persistence may relate to many factors, such as tolerance to environmental stress and resistance to pests and diseases, as well as persistence to frequent defoliation by cutting of forages (Tamaki et al. 2010). In frequent cutting of forages, different forages and their cultivars vary markedly in how their tiller density declines with time (Wilman and Gao 1996). Moreover, weed invasion decreases the quantity and quality of forage swards over time. Persistence of species and cultivars is not easily combined with high yield. Forages are exposed to many environmentally stressful conditions during the production cycle, such as heavy precipitation, frost, freezing temperature, drought and heat. In northern conditions, adaptation to the physical environment becomes the most important factor, and thus survival is more important than competitive ability (Fjellheim et al. 2015). Winter survival has been one of the main objectives in breeding of forage crops for northern areas characterized by harsh winter conditions. Differences in winter survival of species and cultivars matter even in the centre of Finland where most of the forage cultivation is situated. Winter survival is determined by both abiotic and biotic stresses, such as freezing temperatures, water logging, ice encasement, anoxia, snow cover as well as presence of damaging fungi (Pulli 1980, Rognli 2013). For example, breeding of timothy uses material from different geographical origins and thereby improves the cultivars of a particular area by bringing new features to the programme from other areas. Traits vary greatly among latitudinal ecotypes in Nordic countries; the winter hardiness of the southern traits is weaker than that of the northern traits. Northern traits usually have poorer regrowth ability, but the quality of feeds with northern traits is better. The greatest

benefit of the use of the southern traits in the breeding of northern traits is obtained through improvement in the regrowth ability of northern traits (Isolahti 2010).

Breeders have a strong influence on the adaptive capacity of commercial crops. Breeders are inclined to select high-yielding traits under favourable growing conditions, but these traits may not perform well under adverse conditions (Finlay and Wilkinson 1963). Recently, new methods for designing crop ideotypes for future conditions have been developed based on many simulation crop models (Tao et al. 2017). However, due to the notable uncertainties in climate change impacts at the local level (Rötter et al. 2013), we are unable to determine with certainty which crop features will be needed in the future climate and what is the most valuable diversity. Therefore, it may not be possible to consciously maintain features that turn out to be important in unpredictably changing conditions in a privately financed breeding business. Consequently, some traits may be considered useless and could be lost.

The morphological and agronomic traits, the range of germplasm adaptation of each particular area (i.e. farm management and environmental conditions), and the information regarding germplasm potential responsiveness (i.e. the potential to be genetically improved) are all important for breeding purposes (Charmet et al. 1997). Ultimately, yield security is gained through adaptive management by combining the genetic potential influenced by breeders with management options influenced by farmers (e.g. monocropping, mixtures, sowing time, fertilization, liming, irrigation, plant protection). Farmers can manage the response diversity of agroecosystems using both temporal and spatial diversification approaches. Crop rotation is perhaps the most widely adopted temporal diversity strategy, which is defined as 'growing crops in a recurring sequence on the same field' (Thenail et al. 2009). Response diversity can be cultivated temporally in the same field. Diversification in space can be cultivated in different fields as monocrops within a cultivation mosaic of a landscape, region, or the country. At the within-field level, response diversity can be cultivated in the simultaneous cultivation of two or multiple crop species or two or more cultivars of a given crop in time and space via mixtures, relays, strips or rows (Vandermeer 1989). Furthermore, diversification of an agricultural system can also be performed, for example through diversifying production lines (where diversifying crops is one means) or marketing channels of a farm.

1.6 FORAGE PRODUCTION UNDER CLIMATE CHANGE

Global warming may enhance agricultural production in northern Europe, if proper adaptation measures are applied. In Finland, warming is predicted to be the strongest in winter and weakest in summer. The mean temperature of

January may increase in north-eastern Finland by 8–9°C and in the south-west by 6°C according to the A2 scenario for 2070–2099 (higher emissions, higher levels of climate change) (Ruosteenoja et al. 2011). The temperature may increase by 3–4°C throughout Finland in July (Ruosteenoja et al. 2011). A marked prolongation of growing season (in inland areas 40–50 days from 1971–2000 to 2070–2099) is proposed by the A2 scenario (Ruosteenoja et al. 2011) and intensification of the growing season and warmer winter conditions are predicted (Ruosteenoja et al. 2016). The projections of climate change have shown potential positive effects for grass production (yield response 11-14% increase in non-irrigated and irrigated areas), largely as a result of higher growing temperatures (Höglind et al. 2013). Forage production can also benefit from climate change if three annual harvests could be implemented in higher latitudes where currently a short growing season limits the harvesting times to only two annual harvests (Höglind et al. 2013, Virkajärvi et al. 2015). Precipitation is projected to gradually increase by the end of the century in Finland; winters are likely to get wetter, and to a lesser extent precipitation is likely to increase in summer, spring and autumn (Ylhäisi et al. 2010).

Due to the notable uncertainties in climate change impacts, especially locally at the farm level, changes and climate driven instabilities warrant the production of forages in an intensifying manner. Extremes in weather, such as high temperatures, droughts and, by contrast, heavy rain events are likely to be experienced more frequently (Christidis et al. 2014, Ruosteenoja et al. 2011, Ylhäisi et al. 2010, Christensen and Christensen 2007, Trnka et al. 2014). Worsening early summer droughts and heavy rains during the end of summer, autumn and winter are possible (Trnka et al. 20111), and are likely to be harmful to sowing, primary production and the overwintering of forages. Moreover, the projected additional harvest per year may not be manageable if the precipitation during the autumn period increases because soils must be dry enough to carry heavy tractors and because harvesting requires a dry period (a few days) to ensure successful storage of feeds (Höglind et al. 2013).

Winter injury of overwintering forages may become more common (Bélanger et al. 2002, Höglind et al. 2010, Thorsen and Höglind 2010, Peltonen-Sainio et al. 2016), because of less cold hardening of perennial forage crops during autumn (Bélanger et al. 2002) and reduced snow coverage time and thickness of snow, which typically insulate and protect overwintering plants during the harsh winters in Finland (Pulli 1980). Fluctuating winter weather and a lack of hardening due to the unfavourable autumn hardening period (lack of cool temperatures) expose crops to frosts, ice encasement and soil heaving (Bélanger et al. 2002, Thorsen and Höglind 2010, Peltonen-Sainio et al. 2016). However, winter survival is not only affected by climate, but also by many biotic factors (Pulli 1980), for instance, choice of cultivar as well as management of forage swards.

Transforming climate change projections into management strategies despite the uncertainty of predictions is in an early stage of research. The performance of forage production in the face of increasing intensity and frequency of weather extremes is threatened, and management options for climate resilience are lacking. There is an urgent need to explore climate resilience.

1.7 CLIMATE CHANGE IS CAUSING GEOGRAPHICAL SHIFTS IN CROP PRODUCTION

Finland is characterized by large differences in growing conditions between the south, centre and north of the country: cereal production is concentrated in south-west Finland, whereas forage production dominates in central, north and north-east Finland (Virkajärvi et al. 2015). In addition to temperature (day-degrees) accumulation, photoperiodic and precipitation patterns and soil characteristics also vary spatially: clay soils are located in southern and south-western Finland, coarse mineral soils dominate in central and eastern Finland, and organic soils in north and north-east Finland. These soils have divergent agronomic characteristics: clay soils have a high water-holding capacity, where by contrast, coarse mineral soils have a low water-holding capacity, and organic soils are characterized by high water-holding capacity and low thermal conductivity (Mukula and Rantanen 1987). Through choice of crop species, breeding of cultivars, and management, agricultural crop production is able to adapt to prevailing local and regional climate–soil environmental conditions.

Finland is the northernmost agricultural country in the world. A shift in thermal limits is predicted to relocate the effective temperature sum northwards and lengthen the growing season in northern areas where the yield potential of agriculture is currently limited by a short growing season and an insufficient temperature sum. In higher latitude locations, such as Finland, suitability for warm-season crops is likely to increase, and northward extension of cultivation is projected (Tuck et al. 2006, Fronzek and Carter 2007, Peltonen-Sainio et al. 2008, Olesen et al. 2011).

Due to the geographically divided dominance of the main soil types in Finland (III: Fig. 1), changing climate will change the climate–soil combination. The interaction of climate and soils is an important dimension in understanding the need for adaptation (Tuck et al. 2006, Rötter et al. 2013) and requires further attention.

2 AIMS OF THE THESIS

In our published research (I–III) climate resilience was operationalized as the ability of the forage crops to maintain a consistent performance of function when facing change and variation. The focus of my thesis is whether response diversity within species and cultivars of Finnish forage crops reduces yield response variation to weather variability. I chose DM yield (kg ha^{-1} $year^{-1}$) as the key response variable, and set the following specific research questions:

1) How much within-species diversity in response to weather variables exists in Finnish forage crop species?

2) Can response diversity (measured as the number of identifiable response groups of species and cultivars with similar yield responses to weather patterns) be used as an index of response diversity?

3) Does the response diversity index (RD-index) vary from one climate–soil type pattern to another?

3 MATERIALS AND METHODS

3.1 FORAGE CROPS IN THE FINNISH CASE

The study focuses on timothy (*Phleum pratense* L.), meadow fescue (*Festuca pratensis* Huds.), tall fescue (*Festuca arundinacea* Schreb. syn. *Lolium arundinaceum* Schreb.) and tall fescue-type festulolium (*F. arundinacea* Schreb. × *Lolium multiflorum* Lam., i.e. *Festulolium pabulare*) that were backcrossed with *F. arundinacea* (DLF 2016), Italian ryegrass (*Lolium multiflorum* L.) and red clover (*Trifolium pratense* L.). Timothy and meadow fescue are the most important forage species in Finland due to their ability to withstand harsh winter conditions and relatively high yielding ability with good nutritive value (Virkajärvi et al. 2015). Compared to the other forage crops, the regrowth ability and the yield of the second harvest of timothy is lower than other forage crops, particularly *Festuca*-genus forage crops. Tall fescue is increasingly used in Finland because it has good regrowth ability (Virkajärvi et al. 2015) and the use of tall fescue-type festulolium is also increasing, although its winter survival is still insufficient at higher latitudes. Italian ryegrass does not overwinter under Finnish conditions. Red clover is the most important forage legume in Finland. Forages are commonly cultivated in mixtures, and red clover is often used in mixtures with timothy or *Festuca*-genus forage crops (Virkajärvi et al. 2015).

3.2 VARIETY TRIALS DATA AND WEATHER DATA

The results of Official Variety Trials of Natural Resources Institute Finland (previously MTT Agrifood Research Finland) were used (Kangas et al. 2009). The trials followed specified procedures which are described in detail by Kangas et al. (2009), Peltonen-Sainio et al. (2011) and Hakala et al. (2012) and they were carried out in locations all over Finland (Figure 1). Most of the trials were organized by regional research stations of the Natural Resources Institute Finland, but some of the trials were organized by plant breeding companies or private agricultural research stations. Year-round weather data from 1979 to 2012 from the Finnish Meteorological Institute were utilized from the weather stations closest to the Official Variety Trials.

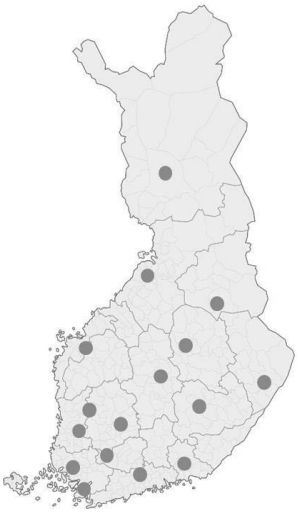

Figure 1 Locations of the Natural Resources Institute Finland Official Variety Trials.

The annual total (cumulative over all harvests) forage crop DM yield (kg ha^{-1} $year^{-1}$) was used throughout as the response variable to weather variability. The DM yield performance was selected as the response variable because it represents the function of forage production most important for providing farm fodder and consequently food supply and farm income. The data consisted of 8361 yield records of annual DM yields for five species and 126 cultivars from 16 different trial sites from 1979 to 2012 (I and III). Regarding the modern cultivars, the trials from 2000 to 2012 provided 1156 records of annual DM yields for 39 modern cultivars (II). Each cultivar was associated with 20 to 70 observations from 11 different trial sites.

Forages were cut 2–3 times per year. Harvesting dates were ranked annually as well as among trials depending on weather conditions and trial locations. After the establishment year, the production cycle of perennial forage stands was between 3 and 4 years, whereas Italian ryegrass was established annually. The number of replicates ranged from 3 to 4. Each year the test set of cultivars gradually changed and control cultivars stayed similar. The size of plots was 7–10 × 1.50 m, depending on location and year. Approximately 1% of the harvesting dates were estimated using a linear mixed model because of missing data. Estimation was based on harvesting dates of the other cultivars at the same trial site and in the same year. The model considered the effects of the site, year, species/cultivar (I and II) and soil type (III).

All experiments were arranged according to a randomized complete block design or an incomplete block design. Fertilizer use in the trials depended on cropping history, soil type and fertility (Kangas et al. 2009, Hakala et al. 2012).

4 ANALYSIS

A flow diagram of the analysis is given in Figure 2, and details are explained step-by-step in the following sections.

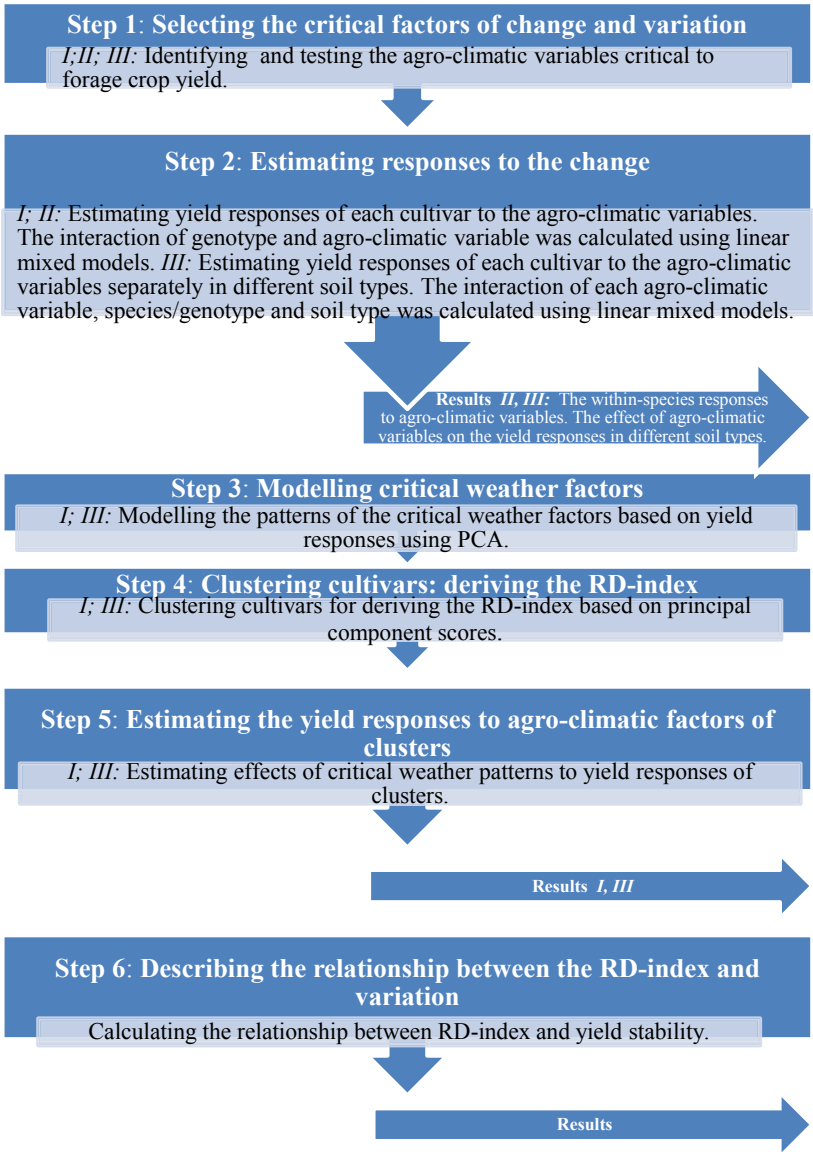

Figure 2 A flow diagram of the analysis.

4.1 STEP 1

The hypothetically critical agro-climatic variables for forage crop yield performance were identified based on previous research (Bélanger et al. 2002, Volenec and Nelson 2007, Thorsen and Höglind 2010) (I: Table 1) and practical knowledge of the research team.

These 35 agro-climatic variables were tested separately related to the fall (autumn) hardening period during which cold hardiness of perennial forage crops is enhanced by cool temperatures (Bélanger et al. 2002), and related to the thermal growth period and the winter period, as proposed by Thorsen and Höglind (2010). The periods were defined as follows: fall hardening started from the last day when the sum of daily difference between 'cold degree days' (below 5°C) and warm 'degree days' (above 5°C) was 0 after the 1st of August and continued to the last day of the first occurrence of minimum air temperatures of ≤ –10°C. The winter period started from the day following the end of the fall hardening and continued to the end of the day before the growth period began, which started from the fifth day of the first 5-day spell when daily mean air temperature exceeded 5°C and ended with the last day of harvest (I).

The yield responses of cultivars were firstly calculated for all the 35 pre-selected agro-climatic variables (I). Based on the statistical significance of the interaction between the cultivar and the agro-climatic variables in terms of yield response (for *p*-values see I: Table 1), but also on other selection criteria (I), 13 agro-climatic variables were retained for further analysis. First of all, variables that had non-significant effects on yield were removed. These included: number of days with maximum temperature of 25°C during growth period, number of days with maximum temperature of 28°C from the start of growth period to 1st cut and from 1st cut to 2nd cut, precipitation sum during growth period, precipitation sum 7 days before 1st cut, precipitation sum 7 days after 1st cut and number of days when frost occurs during spring. The following agro-climatic variables were excluded due to a lack of data: number of days with snow cover during growth period and number of days with snow cover >10 cm during winter period. Finally, the following variables were removed based on model selection criteria of PCA and based on a minor effect on forage crop yield: length of winter period, precipitation sum during winter period, temperature sum during winter period, temperature sum >0°C during growth period, length of growth period, length of growing time from 1st cut to 2nd cut, temperature sum >5°C from 1st cut to 2nd cut, temperature sum 14 days after 1st cut, length of start of growth period to 1st cut, temperature sum >5°C from start of growth period to 1st cut, number of days with maximum temperature of 28°C from 1st cut to 2nd cut, temperature sum accumulation rate from start of growth period to 1st cut, precipitation sum during growth period, precipitation sum from start of growth period to 1st cut.

All five forage crop species and their 126 cultivars were studied over the species (I) and soil types (III), whereas in II, the species (and modern cultivars) were tested separately (i.e. interaction of cultivar genotype (G) × environment (E) (categories of agro-climatic variables) for each species separately). This first approach, comparing the cultivars over the species, was adopted in order to explore whether diversity in yield responses exists within the entire set of forage crop species and cultivars. This approach revealed whether cultivar responses within species differed, but also whether and how they differed compared to crop responses of cultivars of other species.

Note that the average annual DM yield (kg ha^{-1} $year^{-1}$) (the sum of all cuts per year) was used throughout the study as the response variable to weather variability. Thus, it is clear that the DM yield decreases towards the end of the production cycle (the third/fourth year). The production cycle of perennial forage stands is commonly 4–5 years in Finland (Virkajärvi et al. 2015). Re-establishment of forage stands is due to the decrease of productivity over time because of winter damage and weed invasion (Virkajärvi et al. 2015).

4.2 STEP 2

The relationships of weather variables to DM yield were nonlinear in most cases, leading to violations of the assumption of linearity for the regression model. Several weather variables were also strongly correlated, which would have led to a multicollinearity problem in the regression analysis. Hence, weather variables were not used as continuous variables. Instead, new categorical weather variables were generated that classified the observed values into three categories: low, medium and high. The three categories had an equal number of trials in each. 33% (low), 33% (neutral) and 33% (high) of the observations were used in the first round of analysis, where only climatic variables were considered (I, II) (I: Table 1). The interaction of G and E (the agro-climatic variables) was analysed using mixed models (I, II), and the results of the within-species responses to agro-climatic variables were obtained for timothy, meadow fescue, festulolium, tall fescue and red clover (II). The moderate category was conceived to represent the most frequent weather conditions, and low and high categories to represent conditions which will presumably be more frequent in the future. In the second round of analysis, in which soil type was added as an explanatory variable, categories of 45% (low), 10% (neutral) and 45% (high) were used (III), and the three-way interaction of G, soil types and E (the agro-climatic variables) (III) was analysed using mixed models. Three different soil types were used in the analysis: coarse mineral, clay, and organic soils. The smaller neutral category (10%) was selected for the second round of analysis in order to ensure enough data for analysis in each soil type (III). It is possible to use different ratios between categories, based on variation or chosen level of

agro-climatic variable or number of observations per category, for example. All of these options were considered but the last one was selected because a more uneven division of observations was not possible because it would have led to categories with only a few observations for some agro-climatic variables, which would reduce the reliability of yield estimates.

Regarding each cultivar, the difference in yield estimates between extreme categories (high–low) were calculated (I, III). The moderate weather categories were not included in this phase. The calculated values (high–low) were utilized in further analysis in principal component analysis (PCA) and cluster analysis (I, III). It was not assumed that all yield responses were monotonous (the medium class being always between the high and low categories).

4.3 STEP 3

PCA was used to identify a simplified structure that best explained the variance in yield response of the cultivars to the agro-climatic variables. Principal components (PCs) were calculated for the 13 critical individual agro-climatic variables. PCs with eigenvalues greater than one were retained (Cattell and Jaspers 1967). The first PC accounts for most of the variation and the last PC accounts for the least. Four agro-climatic factors (equalling the four PCs) best explaining the yield response variation of the DM yield were used to identify the weather patterns (I). The scoring coefficients and contribution of the individual agro-climatic variables to the agro-climatic factors, i.e. PCs, were reported for all cultivars over the species and soil types (I: Table 2), and for the three soil types separately (III: Table 3).

4.4 STEP 4

To create a measure for response diversity, i.e., response diversity index, the cultivars were clustered using Ward's (1963) hierarchical clustering. Clustering was based on the yield responses to agro-climatic factors over all soil types (I), and for each soil type separately (III). The PC scores formed in Step 3 were used. Squared Euclidean distances between data points were used. The number of clusters was proposed to represent the response diversity for the set of cultivars (I) and for the combination of sets of cultivars and soil types (III).

4.5 STEP 5

It is common to calculate average values for every cluster. However, here, the average yield differences between high and low categories for every PC within every cluster were calculated. The yield response difference was chosen for the calculation instead of average yield because the aim was to focus on the yield response variation (not yield variation in general). Focus could have been on the yield variation in general; however, the yield variation between years is affected by many factors and therefore, it may not be the most exact indicator of climate resilience. By calculating the yield response differences, the focus is on yield variation as a response to weather variation.

In the calculations, weighting was based on PC loadings, which were squared and divided by the eigenvalue of the component. The number of clusters was selected based on the dendrogram, the pseudo t2-criterion and the variation in *r*-squared values (Yeo and Truxillo 2005).

Analysis was carried out with SAS Enterprise Guide 7.1 (SAS Institute Inc., Cary, NC, USA). For further details see I, II and III.

4.6 STEP 6

The relationship between the RD-index and the yield response variation of the forage crops in each of the four weather patterns (PCs) was calculated using the estimated yield responses and their variances of factors for every cluster, calculated in the previous step. The pooled standard deviations, which are the weighted average of standard deviations for several groups (clusters), were calculated for each of the four factors for every value of the RD-index from 1 to 10. Hierarchical clustering made comparison of the values of RD-index interpretative. For example, when nine clusters were compared to ten, only one of the former clusters divided and all the others remained. Thus, it was possible to calculate estimates of yield responses and their variances separately for every value of RD-index. Weighted means and standard deviations were calculated likewise in previous steps when number of clusters divided from ten to one. For example, the first agro-climatic factor (warm growth period) in RD-index=3 had three clusters, for which standard deviations were 785, 822 and 533, respectively.

Because standard deviations for each agro-climatic factor and cluster in every value of RD-index up to ten were calculated, the pooled standard deviations were used as measure of variation. This enabled to analyse the connection between yield stability and RD-index. The equation of pooled standard deviation can be written as follow:

$$\mathrm{sd}_{pooled} = \sqrt{\frac{(n_1 - 1)s_1^2 + (n_2 - 1)s_2^2 + \ldots + (n_k - 1)s_k^2}{n_1 + n_2 + \ldots + n_k - k}}$$

where s is standard deviation of kth cluster and n is number of cultivars of kth cluster.

5 RESULTS AND DISCUSSION

5.1 WITHIN-SPECIES DIVERSITY OF RESPONSES OF THE MODERN SET OF CULTIVARS TO INDIVIDUAL WEATHER VARIABLES

Some amount of diversity in responses within species was recorded, but there were only a few cases (mainly by festulolium, but also by tall fescue) where high response diversity to agro-climatic variables that had a significant effect on yield performance was found (II: Table 3). Overall, the within-species diversity of responses within the modern set of forage crop cultivars was low when compared to those reported within barley cultivars (Hakala et al. 2012). Inclusion of a higher number of cultivars, as exemplified by a higher amount of timothy cultivars, in a cultivar pool or their foreign origin was not sufficient to ensure within-species response diversity to weather (II). Regarding timothy and meadow fescue, gaps in ability of the modern set of cultivars to withstand high temperatures during primary growth (timothy) and a high temperature sum 7 days after the first harvest (meadow fescue) were found (II). The yield penalties of timothy and meadow fescue to temperature stress observed in our study may be explained by their northern origin, and temperatures below 21°C have been suggested as optimal for growth for timothy (Smith 1972, Bertrand et al. 2008). The low within-species response diversity may be explained by Baltic cultivars being highly homogenous in meadow fescue (Fjellheim and Rognli 2005). The outcrossing and hexaploid nature of timothy, as well as gene flow between the cultivars and natural populations, inhibit geographical differentiation (Tanhuanpää and Manninen 2012). It has been assumed that the post-Pleistocene colonization reduced the genetic diversity of species in northern areas relative to central refugia due to the few founder individuals and population bottlenecks, leading to reduced genetic diversity of timothy (Fjellheim et al. 2015). The vernalization requirement in the north (highest in northern populations) together with the required adaptation to northern photoperiodic conditions (longer photoperiodic requirements in northern populations) may explain the differentiation of the northern populations from the European populations (Fjellheim et al. 2015).

All the modern red clover cultivars suffered from both low and high accumulation of warm winter temperatures (II). Yield penalties may be explained by dehardening of red clover because of warm winter temperatures (Bélanger et al. 2002). On the other hand, lack of warm winter temperatures can promote long-standing snow cover and thus enhance crop diseases (clover rot *Sclerotinia trifoliorum* Erikss., and root rot *Fusarium* species (Ylimäki 1967, Yli-Mattila et al. 2010)). Except for the red clover cultivars, cold stress during winter and lack of warm winter temperatures consistently

reduced the yields of all species and cultivars. All the modern cultivars of tall fescue and festulolium suffered from low precipitation during the fall hardening (II). However, festulolium gave a good example of enhanced capacity to adapt to climate change, because a broader range of responses within a species is likely to enhance safe space for adaptation (Hakala et al. 2012, Kühsel and Blüthgen 2015). As a synthetic hybrid, festulolium exemplifies the significance of a diverse genetic basis for response diversity in terms of weather variability. Festulolium hybrids are developed by crossing meadow fescue (*Festuca pratensis* L.) or tall fescue (*F. arundinacea* L.) with perennial ryegrass (*Lolium perenne* L.) or Italian ryegrass (*L. multiflorum* L.). Using perennial ryegrass as a paternal parent in breeding under Finnish conditions should be further investigated for a cultivar with potentially high within-species response diversity, because all the tested cultivars originated from *F. arundinacea* × *L. multiflorum* (DLF 2016) (II). The observed differentiation within *Festulolium* cultivars may be partly explained by the fact that in the breeding of a synthetic hybrid the desired features may be more easily controlled (mixture of parental species equally gives more uniform results) than in grasses like timothy because outcrossing and hexaploid nature of timothy results in a poorly predictable complex mixture of parental genes. However, similar synthetic species hybridization is likely impractical for many other forage species.

5.2 RESPONSE OF FORAGE CROPS AND THEIR CULTIVARS TO CRITICAL WEATHER PATTERNS

Four weather patterns (PCs) (I: Table 2) explained ca 77% of the yield response variation among forage species and cultivars. PCs were described as: PC1 = warm growth period, PC2 = high precipitation during fall hardening and high temperatures before first harvest, PC3 = warm winter, and PC4 = high precipitation after the first harvest and a high number of hardening-supportive cold degree days.

Ten clusters were composed, explaining 78% of the total yield response variation (I: Figs 2 and 3). More detailed information regarding clusters is presented in Table 1.

Table 1 Number of cultivars per cluster (N), mean forage yield (DM kg ha^{-1}), its standard deviation, minimum and maximum yields, and coefficient of variation (CV) of each cluster (%). Clusters refer to I: Figs 2 and 3.

Cluster	N	Mean	Std dev	Min	Max	CV (%)
1	19	8431	401	7727	9645	5
2	38	8692	585	7753	9815	7
3	11	8212	356	7738	9075	4
4	14	7412	576	6250	8417	8
5	13	7912	336	7439	8842	4
6	8	8407	765	7460	9680	9
7	7	8123	511	7373	8974	6
8	4	7634	364	7148	7914	5
9	8	7661	850	6190	8856	11
10	3	9838	252	9553	10029	3

The warm growth period (PC1) explained the most, a quarter, of the forage yield response variation. The response of all the cultivars to this PC ranged from −6% to +13% of the mean yield (I: Fig. 2). This is explained by Finland being the northernmost agricultural country, with specific agronomic characteristics such as a short growing season and low temperature sum accumulation. A warm growth period is therefore a dominant factor to reach the yield potential of most of the forages (I: Fig. 2) (e.g. Pulli 1980, Hakala and Mela 1996, Trnka et al. 2011). In particular, the red clover dominated cluster (CL4) benefitted markedly from a warm growth period (I: Fig. 2), which is in line with the observation of Halling et al. (2004) who reported a high correlation of clover yield with cumulative day-degrees during the regrowth period.

Nearly a quarter of the yield response variation was explained by PC2, high precipitation during fall hardening and warm temperatures before the first harvest (ranging from −6% to +6% of the mean yield). Abundant autumn precipitation was clearly harmful for some forages (CL2, CL3) perhaps because of a greater winter kill due to excessive soil moisture during the autumn hardening period (Paquin and Mehuys 1980). High temperatures in the primary growth period can be either beneficial for cultivars with rapid early season growth ability, or lead to yield penalties for cultivars with northern origin (CL2, CL3) (Sheaffer et al. 1992, Bélanger et al. 2002, Volenec and Nelson 2007) (I: Fig. 2).

Winter conditions in Finland are harsh and fluctuating. Warm winter conditions (PC3) increased yield among most of the clusters, and the response of the mean yield of all the cultivars ranged from −5% to +20%. This PC explained 15% of the yield response variation, showing the importance of warm winters, particularly for the winter-sensitive forages (Thorsen and Höglind 2010). Warm winter conditions affect snow cover and

the effect of snow cover on crop performance is very complex, depending on abiotic (e.g. timing and fluctuation in temperature) and biotic factors (Nissinen 1996). Abiotic winter damages are less prevalent in norther latitudes where a thick and a stable snow cover exist. However, a stable and prolonged snow cover tends to enhance the occurrence of damaging fungi (Nissinen 1996). High temperatures under the snow promote the incidences of fungi (Nissinen 1996). However, if the thaw happens rapidly, water may gather under the snow and this can prevent the growth of fungi. Thaw and a lack of snow cover may on the other hand also promote detrimental ice enhancement. Warm winter weather pattern was clearly the reason dividing red clovers into two main clusters (CL 4 and 8): in contrast to red clover dominated cluster 4, the sole red clover cluster 8 suffered from warm winters (I: Fig 2). This may be associated with sensitivity of some red clover cultivars to the biotic factors to favourable weather conditions: e.g. clover rot (*Sclerotinia trifoliorum* Erikss.) causes damage during winters characterized by a thick and extended snow cover (Ylimäki 1967, Yli-Mattila 2010). Because of the complexity of winter survival and a lack of more specific data (e.g. snow coverage, temperatures under the snow coverage), the explanations for these findings can be only speculated.

Yield response to high precipitation at the regrowth stage and high amount of hardening-supportive cold degree days (PC4) explained 14% of the yield response variation, and the response of the mean yield of all the cultivars ranged from –10% to +10% of the mean yield. Clearly some of the forages, i.e. festulolium and tall fescue cultivars (CL10), were sensitive to high precipitation at the regrowth stage and were not able to take advantage of the high amount of hardening-supportive cold degree days. The high amount of cold degree days may be associated with longer and also possibly earlier autumns, which limits the cuts per year of annual Italian ryegrass, and explains the yield penalties of Italian ryegrass (dominated in CL5). On the other hand, red clover (CL8) and timothy (CL3) benefitted from the high precipitation at the regrowth stage and the high amount of hardening-supportive cold degree days (I: Fig. 2). It seems that these winter harder species can take advantage of chilling temperatures during the fall better than other species.

The findings of PCA indicated that the very similar characteristics of the cultivars result in similar yield responses to different weather variables. It was shown that cultivars either benefitted or suffered from both high precipitation during fall hardening and high temperatures before first harvest as well as high precipitation after the first harvest and a high number of hardening-supportive cold degree days. This may be explained by the construction of the gene base in the breeding process so that the reaction to the combined weather pattern (e.g. high precipitation during fall hardening and high temperatures before first harvest) is either positive or negative. However, these linkages need further research to be fully understood.

5.3 THE RD-INDEX

The value of the RD-index was 10. This index value emerged when all soil types were considered in the analysis (I) and thus it describes the gamma diversity, i.e. the total response diversity to weather of the forage crops and their cultivars in Finland. The species-specific RD-indices are shown in Table 2. Species traits turned out to dominate the yield responses among clusters. An increase in RD-index decreases the yield response variation (Figure 3).

Table 2 *Number of cultivars of forage species divided into clusters that response similarly to the weather patterns and the species-specific RD-index.*

Species	CL 1	CL2	CL3	CL4	CL 5	CL6	CL 7	CL8	CL9	CL10	Total	Species - specific RD-index
Timothy		37	9				5		5		56	4
Meadow fescue	18				1	5	1		1		26	5
Tall fescue	1					1				2	4	4
Festu-lolium				1		1				1	3	3
Italian ryegrass			2		12	1	1				16	4
Red clover		1		13				4	2		20	4
Total	19	38	11	14	13	8	7	4	8	3	125	10

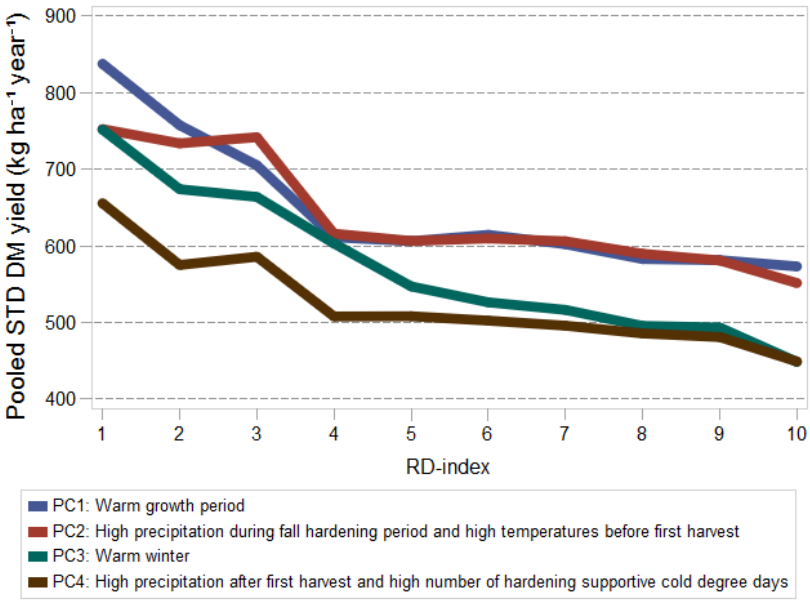

Figure 3 An increase in RD-index decreases the yield response variation (pooled standard deviation, STD) of the forage crops in each weather pattern (PC1-4). Increase in number of clusters is shown on the x-axis where one cluster solution describes the situation where all cultivars (126 cultivars) belong to the same cluster. The 10 cluster solution describes the 10 RD-index solution used.

5.4 INTERACTION OF SOIL TYPE AND WEATHER PATTERNS IN YIELD RESPONSE AND THE RD-INDEX IN DIFFERENT SOIL TYPES

The effect of weather patterns captured by the four PCs (I) were associated with soil types (III: Table 3). Loadings of the critical climatic variables of the weather pattern captured by the first PC (I), warm growth period, correlated (r = 0.70) with the loadings of these variables in the first PC for the data for clay soils. The PC that explained the most variation in clay soils actually contained the very same individual agro-climatic variables as the PC 'warm growth period' in the analysis across the soil types (I). This tight correlation, even if the clay soils are generally considered drought-prone, might best be explained by the ability of forage crops to benefit from warmer growth conditions due to the relatively well-developed root systems of forage crops together with the high water-retention capacity of clay soil. On the contrary, the high precipitation during fall hardening or during the regrowth stage was found to be generally detrimental to forage crops in clay soils, which might be explained by the heavy compacting nature and therefore slow water infiltration and proneness to flooding of clay soils (Mukula and Rantanen 1987).

In organic soils, the correlation of the first PC was 0.78 with PC1 warm growth period. The importance of the warm growth period for the forage crop yield performance in organic soils is known from previous studies (Mukula and Rantanen 1987). Organic soils are called 'cold soils' in Finland and they are characterized by low thermal conductivity, particularly when drying (Mukula and Rantanen 1987).

The PC explaining most of the variation of coarse mineral soils correlated slightly with the 'high precipitation during fall hardening and high temperatures before first harvest' (r = 0.52) and 'warm winter' (r = 0.46) of PCs 2 and 3, respectively. This showed that high precipitation during fall hardening can actually be beneficial in coarse mineral soils because fall hardening prevents soil moisture from becoming high enough to have negative consequences on yield performance (Paquin and Mehuys 1980), while enhancing soil moisture in the spring that otherwise might rapidly start to limit growth in those soils.

Although warm winter temperatures increased yields in clay and organic soils, for coarse mineral soils the frequent occurrence of thaw days during winter appeared to be harmful. This is explained by proneness to ground frost of those soils, which causes root damage.

Crop responses and response diversity of forage crops and their cultivars varied between soil types (III). Response diversity measured as number of identifiable functional groups of species and cultivars with similar yield responses varied from one climate–soil type pattern to another: RD-index values were 4 for coarse mineral soils, 9 for clay, and 8 for organic soils (III).

5.5 RESPONSE DIVERSITY TO GUIDE PRACTICAL MANAGEMENT

The proposed response diversity assessment can serve as a practical tool to manage the performance of forage crop production in variability in weather and in the face of climate change. The seasonal and, in perennial forages, cumulative over-the-seasons yield performance of forage crops, and the yield security, can be enhanced by combining species and cultivars with complementary responses to the critical weather patterns. Complementary cultivars can be cultivated in different fields or in the same field, and using both temporal and spatial approaches for diversification:

- Combining complementary responses of cultivars as crop rotations.
- Spatial diversity can be implemented both at landscape-level (between the parcels) and at within-parcel level (in analogy to mixed monocropping; Brooker et al. 2015): combining complementary responses of cultivars in different fields within a cultivation mosaic of a farm, within the cropped landscape, within the cropped region or within the entire country.
- Combining complementary responses of cultivars within-field through mixtures, relays, strips or rows (in analogy to intercropping, which is simultaneous cultivation of two or multiple crop species or cultivars as one crop stand; Vandermeer 1989).

From a farmer's perspective, spatial diversification is the most important because annual yield loss and yield variation have negative consequences due to the costs of supplementary feeds. Furthermore, re-establishment of swards and moreover forage feeds are not entirely, at least not cost-effectively, substitutable through the market.

Note that the results reported in this thesis do not incorporate many biotic factors that may affect response diversity in intercropping, as the data (and hence the clusters) are from sole-crop cultivar field tests. Thus, it is important to further explore how interactions and biotic (and also many other abiotic) factors synergistically affect response diversity. This means interactions in terms of competition (De Wit and Van den Bergh 1965, Harper 1977, Spitters 1983, Creissen et al. 2013), facilitation and compensation (Vandermeer 1989, Hartley and Amos 1999, Kirwan et al. 2007, Ergon et al. 2016) and their effect on response diversity. There exists positive evidence regarding forage grass–legume interactions (Vandermeer 1989, Kirwan et al. 2007), especially under low nitrogen fertilization (Ergon et al. 2016). The mixing effect of grass–grass or legume–legume is less clear (Nissinen and Hakkola 1994), although synergistic effects have been reported in such mixtures as well (Hooper and Dukes 2004, Ergon et al. 2016). Furthermore, the competitive balance in a community is affected by many abiotic and biotic factors, and thus a particular species can turn out to be

functionally less important (functional dormancy) in a given time when the function is maintained by another species (functional compensation) (Hartley and Amos 1999). Agricultural fields represent relatively closed systems, meaning that compensatory mechanisms mostly occur between the originally sown cultivars and species, even if at ageing of perennial forages contribution of weeds to total productivity increases. Although mixtures represent the most common form of forage production in Finland, the potential of response diversity as a resilience enhancement strategy would be advantageous if considered in the design of mixtures (or other intercrop options) by seed suppliers and farmers as well as in breeding of cultivars more widely. Due to the short growing season and long day conditions in Finland, there is very little difference in heading days within forage species and cultivars that enables cultivating them as mixtures (Virkajärvi et al. 2015, Kangas et al. 2009). Use of planned response diversity for mixtures of cultivars needs empirical testing, which these results may give insight to.

5.6 RESPONSE DIVERSITY IN THE FACE OF CLIMATE CHANGE

Strategies for capacity building to adapt to plausible changes in climate are required in the face of the intensified variability, extremes (Coumou and Rahmstorf 2012) and uncertainty (Rötter et al. 2013) of climate change. The proposed response diversity assessment can serve to enhance climate resilience. It complements the globally prevalent strategies to 'predict and adapt' to long-term average changes in climate (Dessai et al. 2007). This thesis has shown the diversity in differences in response within an economically important group of production organisms, namely between and within species of forage crops, to change and variation in climate. Furthermore, this thesis has shown that this diversity reduces yield response variability, i.e. increases yield stability against weather variability, of mean yield of the sole crops of the set of species and cultivars in question. The findings of this thesis are in agreement with the general hypothesis of the importance of response diversity to the functioning of the system in the face of environmental disturbance (e.g. Walker et al. 1999, Elmqvist et al. 2003, Kühsel and Blüthgen 2015).

To illustrate the difference between species diversity and RD-index, three hypothetical farms cultivating the same total area of a field but with different cultivars are shown in Figure 4. It is possible to have a high diversity of species but still be more unstable in variable weather (Figure 4). This does not mean that all other diversity is unnecessary. It is clear that against a given assessment criterion, or single function, there is an enormous amount of apparent redundancy whose value for humanity is still unclear and may in the future turn out to be critically important. But rather, this shifts the focus

from the maximization of species richness as the optimal insurance of managed systems in the face of global change. It is likely to be more valuable to improve our understanding regarding the response diversity of species, cultivars, or genotypes responsible for a similar function within a system than to focus on the number of species or cultivars or genotypes. Of particular interest is the degree of difference in essential terms, whether it concerns functional characteristics or response characteristics as one specific function.

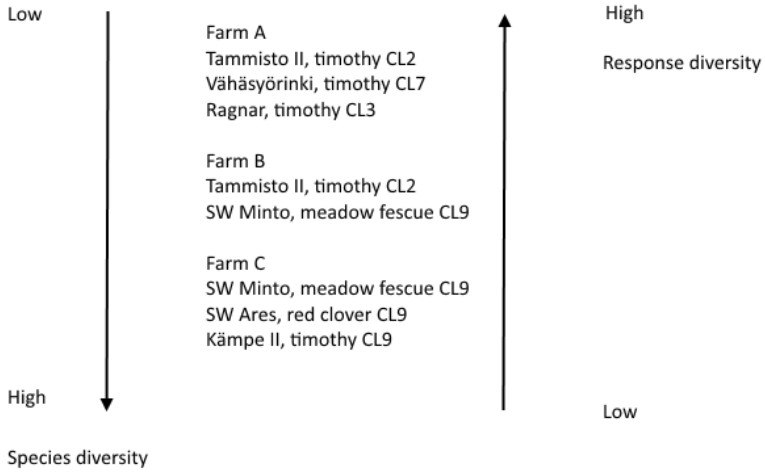

Figure 4 Illustration of the difference between the number of species and response diversity. Cluster (CL) and cultivar names refers to I: Fig. 2, 3. Within the same cluster, cultivars react similarly to weather. The higher the RD-index, the higher the likelihood of yield response stability (decreased yield response variation).

5.7 SOIL TYPE SHOULD BE CONSIDERED IN ADAPTATION

Shifts and northward extension of agriculture are likely to lead to rapid changes in agriculture in higher latitude conditions (Newman 1980, Mills 1994, Carter and Saarikko 1996, Brklacich et al. 1998, Audsley et al. 2006, Peltonen-Sainio et al. 2008). Many of the current studies focus on the climatic limits for a certain crop under different climate scenarios (Newman 1980, Parry et al. 1989), and thus projections of which crops will actually

shift are uncertain. Land-use change is very dependent on how the climate will actually change regionally, with the adaptation further driven by both environmental and socio-economic factors (cf. Nabuurs et al. 2000, Rounsevell et al. 2003, Audsley et al. 2006, Elsgaard et al. 2012). In farming, adaptation is about individual farmers adopting novel species, novel cultivars and new management practices within their farms (Mäkinen et al. 2017), and weather conditions have been reported to have a strong influence on land-use change in agriculture (Peltonen-Sainio et al. 2013). Currently, forage production is concentrated in coarse mineral soils, but organic soils may increase in importance if the extent of cultivable areas for the many currently major and also novel crops increases markedly in central and north-east Finland (Peltonen-Sainio et al. 2008). Increase in grass cultivation in agricultural peat and mull soils may also be promoted by mitigation policies because increased grass cultivation and raised groundwater table in grass cultivation are potential mitigation measures (Regina et al. 2004, Regina et al. 2015).

Breeding and management adaptation in crop production systems focuses on the climate–soil–crop triangle (Figure 5). The results showing the dependence of RD-index on soil type (III) highlight the significance of the soil–climate combination when aiming to increase adaptive capacity through diversity of forage crop yield responses. Because the RD-index was clearly lower in coarse mineral soils than in clay or organic soils (III), this finding may indicate a narrower ability to cope with climate change within forage crops in coarse mineral soils (III).

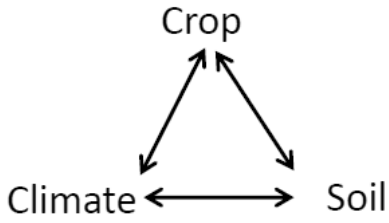

Figure 5 The climate–soil–crop triangle: interdependencies in focus for genetic and management adaptation of crop production in the face of climate change.

5.8 FUTURE RESEARCH

The next logical step in the analysis would be to describe how the RD-index explains the dependence of the yield response variation in each soil type separately, as the interaction of soil–crop response was so clear: different RD-index values were found for different soil types, and different sets of cultivars formed the soil type specific clusters. Validating models with on-farm yield results is another logical step to take (Kahiluoto et al. 2014). The following topics may be useful to study:

- Achieving resilience at the farm level through response diversity may increase costs (in the short-term through foregone yield in optimal growing season for instance). Therefore, the economic costs of response diversity as a risk management strategy of a farm should be evaluated further and could be compared to other risk management strategies. For instance, farmers can secure sufficiency of forage feeds by increasing the storage capacity of feeds, the amount of fertiliser (higher amount of fertiliser can be applied if the quantity or quality yield of the first cut is poor) as well as by having extra land (the needed grass land area may be determined by the lowest expected yield level (Kässi et al. 2015)).
- The nutritional value of the forages (especially digestibility) is critical for feeding and thus recommended to be assessed. Similar assessment as used here could be further conducted using digestibility as the response variable and assessing the response to variables critical for digestibility such as temperature, photoperiod and time of harvest (Bertrand et al. 2008).

In analogy to the RD-indices constructed here, RD-indices can be constructed for management of resilience in other systems and at higher system levels within food systems, and perhaps beyond agroecology, such as in the field of conservation management or in the field of economics. The added value of such applications needs to be evaluated on a case-by-case basis. The presented method quantifies response diversity in an empirical index: such an approach requires empirical data. Long-term datasets, such as those used here, are the cornerstone for such assessments and for adapting agricultural production to climate change.

5.9 LIMITATIONS AND ALTERNATIVE APPROACHES

This dissertation has focused on the response diversity of a specific subsystem of a wider agri-food system. The theories of importance of response diversity to system resilience at all system levels, up to complex socioecological systems, state that a general resilience approach does not attempt to identify changes or shocks that the system may face and thus refers to coping with uncertainty or the unknown. This contrasts with

approaches that identify an expected change or shocks in which there is a danger of narrowing too much, leaving the system vulnerable to the unknown (Carpenter et al. 2001, Folke et al. 2010). Since it is empirically only possible to rely on past and current data, and therefore past and current conditions, generalization to the future is not possible without uncertainty. For example, it is probable that weather variability will be more extreme and frequent than in the past, and the response diversity identified based on past data may not reflect the conditions in the future and thus not ensure resilience when the system faces entirely new climate–soil combinations. The highest possible existing response diversity is not a guarantee of maintaining performance in the new conditions, which may require new types of response features. This limitation leads to the need to value redundancy.

Uncertainty in climate change in the present study was considered in such a manner that cultivars were not selected to provide insurance against climate change in a particular 'most likely' climate change scenario, but rather to perform well irrespective of the direction of change in climate, i.e. cultivars were clustered based on the yield responses to real historical weather variability. Probability of changes in climate (for instance according to CMIP5 which is a model ensemble used for the IPCC's Fifth Assessment Report (Stocker et al. 2013)) represent options to be studied further. Through the assessment of response diversity, the danger in adaptation management to pay too much attention to a particular single driver of change, such as very high temperatures, can be avoided. Focus on a single, 'predicted' disadvantageous change can result in unwanted management outcomes in breeding if it leads to losing response diversity to some novel feature, or if ability to cope with high temperatures turns out to be unimportant in the future climate. Predicting in which climate–soil combinations we need to improve response diversity in breeding now for future purposes is impossible, especially because of the extensive local variation in the projected weather depending on the scenario (Rötter et al. 2013, Trnka et al. 2014). Hence, there are no easy answers regarding the optimal response diversity for yield security or for ensuring the adaptation of species in future local weather, but the approach needs to be continuously applied while the future conditions evolve. Notwithstanding this, management of yield security to withstand climate change at a manageable low subsystems level, such as forage production for example, through the RD-index can result in aggregating resilience over the entire system, including at a higher system level up to the global food system (Folke et al. 2010).

Regarding the methodological choices, PCA is not the only appropriate methodology for the assessment of response diversity. Multivariate clustering analyses or other ordination methods could have been applied (see Laliberte et al. 2010). Clustering seeks to find homogenous groups in the data where the within-group similarity is high compared to the similarities between groups. Instead of maximizing the dissimilarities, the goal of PCA is

to find the most dominant patterns of variability (maximizing variance), in this case the dominant patterns of variability in climate for the yield response variation of the DM yield. Regarding direct clustering approaches (e.g. Kahiluoto et al. 2014), it is likely that the dominant patterns that could be identified by PCA are those that separate homogenous groups in clusters, but by applying the direct clustering approach the most dominant patterns of variability are not explicitly identified and therefore not able to be used in the interpretation of the results. PCA was found to be important in the interpretation and illustration of the practical significance of crop response in each cluster (I).

It is clear that response diversity is dependent on the used agro-climatic variables (I, III). Despite the fact that a high number of agro-climatic variables (35) were tested, of which 13 explained ca 77% of the yield response variation, there are probably agro-climatic variables that would had been suitable but were not included in the current study. For example, there was not enough data regarding the number of days with snow cover during winter period that perhaps greatly indicates the sensitivity of forage crop cultivars to winter damages.

A few limitations relate to the calculation of the significance of G × E in (II): there is a possibility of a high within-cultivar level response diversity and plasticity that leads to high robustness of the cultivars to weather. This means that cultivars are equally robust and high yielding, irrespective of weather conditions. Such potential within-cultivar level response diversity is also important for adaptive capacity, although this type of response diversity was not at the centre of interest in the methodology used and is therefore one aspect that can be considered further. The approach used is justified because more plasticity can be bred within a set of cultivars than within a single cultivar and it is likely that sufficient plasticity under climate change may not be bred within a single cultivar but rather within the entire cultivar or species pool, and we cannot predict which features in a cultivar pool will be important in a future climate. Furthermore, in studying the significance of G × E interaction and gaps in the adaptive capacity of a cultivar pool (cases when G × E was not significant but when the main effect of E was significant), even if the main effect of the agro-climatic variable was not significant in some cases, it is possible that the main effect will in the future become significant. Therefore, it is important to consider the general diversity of responses within the cultivar pool also in cases where E was not significant in the current study (II).

6 CONCLUSIONS

Under climate change, combining strategies that complement traditional adaptation to projected average long-term change in climate with strategies that acknowledge the existing uncertainty in climate change and that enhance coping capacity are required. This thesis shifts the focus from average weather to weather variability and extremes, and from short-term priorities towards the long-term, proposing a strategy to 1) maintain the current forage production function, and 2) safeguard adaptation of crops to uncertainty and disturbances driven by climate change by allowing and enhancing response diversity within species or within crops contributing in a similar manner to the forage production function. The perspective of this thesis is useful for the development of strategies to adapt to the current and changing conditions within agri-food systems and perhaps beyond. The conclusions are summarized as follows:

- Response diversity assessment can be used as a tool for agri-food system actors to manage climate resilience.
- The proposed response diversity assessment and RD-index can be used to reduce yield response variation over seasonal weather patterns.
- Response diversity is not directly positively linked to species richness; the RD-index is more effective than the number of species or cultivars for indicating resilience of yields to changes and variation in climate.
- The assessment of response diversity within species can increase the adaptive capacity of crops, and it can be used as an approach to assess gaps in the adaptive capacity of the cultivar pool and its weak points under climate change.
- The assessment underlines the significance of soil type to the response diversity. The climate–soil–crop triangle should be considered in the planning and implementation of adaptation in agriculture, particularly by farm managers and plant breeders.

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